Inc., and other landowners allowed placement of nest boxes on their properties.

RESUMEN.—Un estudio de 13 años (1979–91), sobre *Falco sparverius* nidifcando en cajas anideras, promedió 4.13 juveniles marcados por nido exitoso; con un 70% estimado de cajas anideras exitosas. El número de juveniles por nido exitoso varió entre años pero no significativamente del promedio de 13 años. El 67% de las cajas anideras fue reocupado en dos o más años sucesivos. La mediana de la distancia de dispersión para hembras $N = 7$) fue de 30 km y 16 km para machos ($N = 3$).

[Traducción de Ivan Lazo]

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SEX-SPECIFIC DIET ANALYSIS OF THE TAWNY OWL (*Strix aluco*) IN NORWAY

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KEY WORDS: *Norway; sex-specific diet;* Strix aluco; *tawny owl*

The diet of the tawny owl (*Strix aluco*) is well-known and, based on pellet analysis, shows broad variation (Mikkola 1983). However, some aspects like the invertebrate content (Cramp 1985) and sexual differences in prey choice (Bildstein 1992) are not expressed by pellet analysis. Digestion hampers identification of invertebrate species eaten, and makes it impossible to estimate the proportion of invertebrates present (e.g., Kirk 1992). A possible difference in diet between the sexes might arise from a mechanism advanced to explain reversed sexual dimorphism (RSD) in raptors (Andersson and Norberg 1981, Lundberg 1986). Females may reduce competition for food with males by taking larger prey than their smaller mates (e.g., Earhart and Johnson 1970); tawny owl females weigh 26% more than males on average (Hirons et al. 1984). However, this is difficult to verify by pellet examination since it is impossible to distinguish between pellets from males and females.

Stomach analysis may be a way to answer these questions provided that prey remains are intact (Hagen 1952, Cramp 1985). Our objectives were (1) to evaluate sexual differences in tawny owl diet, and (2) to quantify the invertebrate prey in the tawny owl diet.

METHODS

During 1987–93, 215 tawny owls, mainly killed in road accidents, were collected in southern Norway. The date of the find was recorded, the sex was determined by inspecting sex organs, and stomach contents were investigated. In 39% (39 males and 45 females), stomachs were empty. The remaining 61% (39 males and 93 females) contained at least one prey item. Reference collections were used to identify the prey remains. Vertebrates were counted directly when intact, or by using skulls and dentaries of mammals and skulls and mandibles of birds. Likewise, invertebrates were counted when intact, but occasionally by compiling remains if partially digested. The biomass of vertebrates was calculated by multiplying the respective average individual weight given in the literature by the number of individuals recorded for each species. The biomass of the invertebrates was mainly calculated by totalling the individual weights of prey items weighed, but values given in the literature were sometimes used.

Prey items were sorted into categories of increasing body weight. Because many (up to 18) invertebrates were present in a single stomach, only their occurrence in each stomach was counted in the numeric distribution (all were represented in the biomass distribution). For testing the numeric size distribution of prey, the Mann-Whitney U-test was used, except when testing male versus female diet where a chi-square test was the most appropriate. To compare our results with previous studies of tawny owl diets, the importance of prey species is expressed in two ways: (1) the percentage biomass of each species among all species recorded, and (2) the numerical occurrence of prey species.

RESULTS

A higher proportion of females than males contained prey in their stomachs ($\chi^2 = 5.63$, $P < 0.05$). Invertebrates comprised 2.7% of the total biomass and 41.6% of the prey by number (Table 1). Lepidoptera, mostly *Noctua pronuba* larvae, dominated both by biomass (2.5%) and numerically (37.2%). Stomachs of females in particular were filled with Lepidoptera, although no significant difference was found between males and females overall (Mann-Whitney $U = 21.5$, $P > 0.05$).

The distribution of different size prey differed significantly between males and females ($\chi^2 = 10.83$, $P < 0.05$).

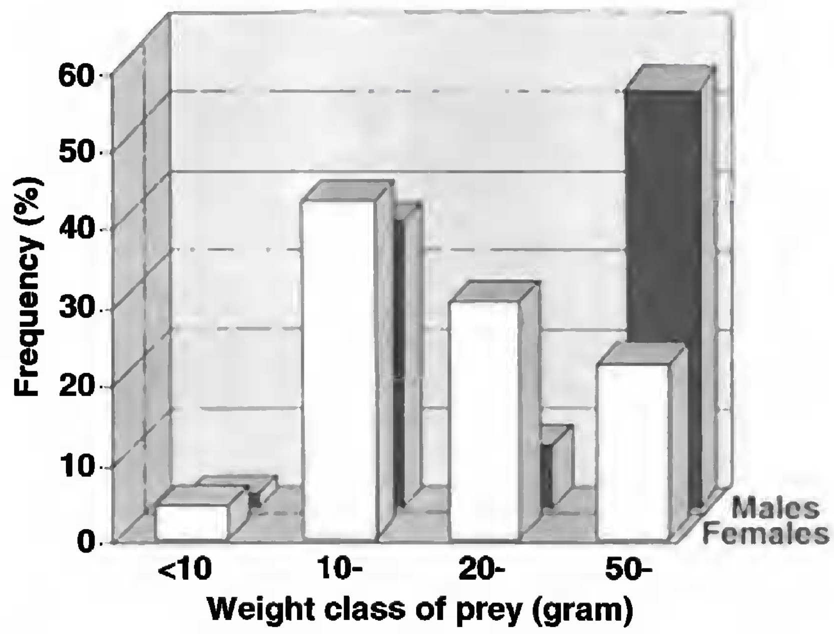

Figure 1. Prey mass distribution in the diet of Norwegian tawny owls.

Females diets' were over-represented with 20–30 g animals such as the field vole (*Microtus agrestis*), but males took more of the heaviest items (Norway rat, *Rattus norvegicus,* and birds). In regard to biomass distribution, 49% of the prey of males were in the heaviest prey group, although many prey were small- to medium-sized, with another peak (33%) at 15–19 g (Fig. 1). Females obtained 64% of their prey by weight from intermediate items (15–29 g), with a minor secondary peak in the heaviest prey (16%). Overall, small mammals predominated while birds accounted for approximately one-third of the diet biomass.

DISCUSSION

Previous studies lacked complete calculation of the biomass of invertebrates. Compared with 2.7% in our study, Labes (1990) found Coleoptera to be represented by <0.3% and Galeotii et al. (1991) reported Arthropods constituting 0.5% of tawny owl prey biomass. Most of the invertebrates in our specimens were identified as larvae of *Noctua pronuba,* which may occur in large numbers in southern Norway (Skou 1991). Even though invertebrates represented a small part of the total prey biomass, the stomachs of 27.3% of owls that had preyed upon larvae contained six or more items (range 6–19), thus perhaps indicating the periodic importance of this prey.

Southern (1968) found that 57% of 239 invertebrates recorded were beetles (*Carabus*) and 29% earthworms (*Lumbricus terrestris*). We found that 42% of the total prey ($N = 269$) in our study were invertebrates, differing little from Southern's results. However, small mammals and birds predominated as prey of Norwegian tawny owls, and males more than females preyed upon the heaviest items.

According to Snyder and Wiley (1976), the degree of RSD in a species shows a strong relationship with the proportional occurrence of birds in the diet. Two other trends correlate with a high degree of RSD—the prey is increasingly active and agile (Newton 1979) and larger relative to the predators (von Schantz and Nilsson 1981). Both these relationships mean that smaller body size will be favored since the prey requires more search and pursuit

Table 1. Prey items ($N = 269$) from stomach analyses of 131 Norwegian tawny owls (males: 13 stomachs from the summer and 25 from the winter; females: 39 from the summer and 54 from the winter). Summer represents the period from 15 April to 14 October and winter the period from 15 October to 14 April. (N) represents number of items and (B) the biomass of that item with respect to total biomass.

			Male				Female			
Prey	Ref.	Mass (g)	*N* Summer	*N* Winter	Sum (g)	*B* %	*N* Summer	*N* Winter	Sum (g)	*B* %
Mammals										
Clethrionomys glareolus	a	16.00	3	5	128.0	3.27	6	9	240.0	6.14
Microtus agrestis	a	21.00	1	3	84.0	2.15	12	18	630.0	16.11
Sylvaemus flavicollis	a	18.00	2	8	180.0	4.60	15	11	468.0	11.97
Mus musculus	a,b	15.00	1	0	15.0	0.38	0	4	60.0	1.53
Sorex araneus	a,b	10.00	3	2	50.0	1.28	6	5	110.0	2.81
Neomys fodiens	a	10.00	0	0	0.0	0.00	0	1	10.0	0.26
Rattus norvegicus	a	100.00	0	3	300.0	7.67	0	0	0.0	0.00
Unident. voles	g	17.50	3	5	140.0	3.58	5	6	192.5	4.92
Subtotal mammals			13	26	897.0	22.93	44	54	1710.5	43.73
Birds										
Regulus regulus	e	5.30	0	2	10.6	0.27	0	1	5.3	0.14
Turdus merula	e	93.20	0	0	0.0	0.00	1	0	93.2	2.38
Unident. *Turdus* spp.	f	100.00	1	3	400.0	10.23	2	2	400.0	10.23
Unident. Passeriformes	f	31.00	1	0	31.0	0.79	2	2	124.0	3.17
Glaucidium passerinum	e	60.00	0	1	60.0	1.53	0	1	60.0	1.53
Subtotal birds			2	6	501.6	12.83	5	6	682.5	17.45
Amphibians										
Bufo sp.	h	10.00	1	0	10.0	0.26	0	0	0.0	0.00
Subtotal amphibians			1	0	10.0	0.26	0	0	0.0	0.00
Invertebrates										
Melolontha vulgaris	c	0.92	2 (1)[i]	1 (1)	2.8	0.07	0	0	0.0	0.00
Cetonia	h	1.00	1 (1)	0	1.0	0.03	1 (1)	0	1.0	0.03
C septemunctata	h	0.20	1 (1)	0	0.2	0.01	0	0	0.0	0.00
Coleoptera	c	0.50	0	2 (1)	1.0	0.03	0	1 (1)	0.5	0.01
Saltatoria	h	1.00	0	0	0.0	0.00	2 (2)	1 (1)	3.0	0.08
Lepidoptera	d,h	1.00	3 (1)	4 (2)	7.0	0.18	61 (9)	32 (10)	93.0	2.38
Subtotal invertebrates			7 (4)	7 (4)	12.0	0.31	64 (12)	34 (12)	97.5	2.49

[a] Nilsson (1981).
[b] Jäderholm (1987).
[c] Labes (1990).
[d] Linné (1758).
[e] Haftorn (1971).
[f] Haftorn (1971).
[g] Average of the most common four identified mammal species.
[h] This study-mass from the stomach analyses.
[i] Parenthetical values represent the number of stomachs containing the prey item.

(Temeles 1985). This view is in accordance with our data—males preyed upon relatively large prey (Norway rats and birds) significantly more than did females. Two more aspects imply that there are real differences between the sexes of tawny owls. Firstly, birds may be difficult to catch; hence, it may be risky for the male to specialize on them. This may lead to more empty stomachs in males than in the females, as our data indicate. Secondly, males with prey items in their stomach carried more prey mass than females (37.4 g vs. 29.5 g), despite the larger size of the female. This may imply that when the male is successful the average prey is larger than that of the female.

However, most of the sparse sex-specific owl diet data available fails to support the prediction of sexual differences in feeding niches, perhaps partly because the species studied fed chiefly on voles which provide little variety in size classes (Mikkola 1983, Wiklund and Stigh 1983). The broad diet of the tawny owl, including a large proportion of birds of various sizes, may permit more size partitioning in prey utilization than in some other owl species. In their review, Snyder and Wiley (1976) concluded that RSD in raptors is more likely to be related to advantages conferred on larger females in terms of copulation, incubation, brooding, and nest defense. The advantage of the smaller male, however, may lie in hunting habits (e.g., Earhart and Johnson 1970, Mendelsohn 1986).

Ideally, to test whether males and females select different prey, the diets of pairs which have the same prey available to them should be studied. This would include intensive radiotelemetry studies and sampling of pellets from individual roosting sites, together with close monitoring of density and dynamism in relevant prey species.

RESUMEN.—Verificación del porcentaje de invertebrados en la dieta, así como la posible diferencia entre los sexos con relación a la selección de presa, fue el objetivo durante el análisis del contenido estomacal de 131 cárabos (*Strix aluco*) de Noruega, de sexo conocido y matados accidentalmente. Invertebrados, sobre todo especies de *Lepidoptera,* tales como *Noctua pronuba,* constituyeron el 2.7% de la biomasa total. No se encontró ninguna differencia entre los sexos con relación a esta parte de la dieta. Generalmente hablando, la biomasa de presa fue dominada por pequeños mamíferos (66.6%) y pájaros (30.2%). Se descubrieron diferencias significantes, debido a que los machos se alimentan relativamente más de los animales más pesados (100 gramos o más), comparado con las hembras, incluyendo en particular la rata parda (*Rattus norvegicus*) y especies de *Turdus,* los cuales representaron un 49% de la dieta de los machos, comparado con un 16% para las hembras, en términos de biomasa. Las hembras obtuvieron el 64% de su alimentación, en términos de peso, de animales de tamaño mediano (15–29 gramos). Animales de este tamaño también formaron una parte importante de la dieta de los machos.

[Traducción de J.R.S. Sciaba]

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